

A NEW SPECIES OF SAGE-GROUSE  
(PHASIANIDAE: *CENTROCERCUS*) FROM  
SOUTHWESTERN COLORADO

JESSICA R. YOUNG,<sup>1,7</sup> CLAIT E. BRAUN,<sup>2,6</sup> SARA J. OYLER-McCANCE,<sup>3,4</sup>  
JERRY W. HUPP,<sup>5</sup> AND TOM W. QUINN<sup>4</sup>

**ABSTRACT.**—The Gunnison Sage-Grouse (*Centrocercus minimus*) is described as a new species from southwestern Colorado and contrasted with the Sage-Grouse (*Centrocercus urophasianus*) from northern Colorado and western North America. Gunnison Sage-Grouse differ from all other described sage-grouse (*C. u. urophasianus*, *C. u. phaios*) in morphological measurements, plumage, courtship display, and genetics. The species currently is limited to 8 isolated populations in southwestern Colorado and adjacent San Juan County, Utah. Total estimated spring breeding population is fewer than 5000 individuals with the largest population (<3000) in the Gunnison Basin (Gunnison and Saguache counties), Colorado. Received 3 February 2000, accepted 29 June 2000.

Sage-Grouse (*Centrocercus urophasianus*; Phasianidae; Tetraoninae) occur only in North America, and historically occupied suitable shrub-steppe habitats from eastern California, Oregon, Washington, and southeastern British Columbia east into western North Dakota, South Dakota, northwestern Nebraska, southwestern Kansas, and adjacent Oklahoma (Aldrich and Duvall 1955, Aldrich 1963, Johnsgard 1973). The former distribution included portions of 16 states and 3 Canadian provinces. These grouse have been extirpated from 5 states (Arizona, Kansas, Nebraska, New Mexico, Oklahoma) and 1 province (British Columbia; Braun 1998).

Two races of sage-grouse have been de-

scribed previously. *Centrocercus urophasianus phaios* is restricted to the area immediately east of the Cascade Mountains in Oregon, north into Washington and south into extreme northeastern California (Aldrich 1946). *Centrocercus urophasianus urophasianus* was reported to occur throughout the remainder of the range (Aldrich and Duvall 1955, American Ornithologists' Union 1957, Aldrich 1963).

Management activities by the Colorado Division of Wildlife to increase the knowledge about sage-grouse within the state resulted in systematic collection of wings from hunter harvest throughout the state starting in the mid-1970s. In 1977, wings from birds in the Gunnison Basin (Gunnison and Saguache counties) were noted to be smaller (based on measurements of primaries 10, 9, and 1) than wings obtained elsewhere in the state. Subsequent studies of grouse in the Gunnison Basin in the mid-1980s (Hupp 1987) and early 1990s (Young 1994) revealed significant differences in morphometrics (Hupp and Braun 1991), breeding behavior, and plumage (Young et al. 1994) compared to other populations of sage-grouse. Recent studies of the mitochondrial and nuclear allele frequencies of sage-grouse in Colorado have revealed additional significant differences (Kahn et al. 1999, Oyler-McCance et al. 1999).

<sup>1</sup> Dept. of Natural and Environmental Sciences, Western State College of Colorado, Gunnison, CO 81231.

<sup>2</sup> Colorado Division of Wildlife, 317 West Prospect Rd., Fort Collins, CO 80526.

<sup>3</sup> U.S. Geological Survey, Midcontinent Ecological Sciences Center, 4512 McMurray Ave., Fort Collins, CO 80525.

<sup>4</sup> Dept. of Biological Sciences, Univ. of Denver, Denver, CO 80208.

<sup>5</sup> Alaska Biological Science Center, U.S. Geological Survey, 1011 East Tudor Rd., Anchorage, AK 99503.

<sup>6</sup> Present address: GROUSE INC., 5572 North Ventana Vista Rd., Tucson, AZ 85750.

<sup>7</sup> Corresponding author; E-mail: jyoung@western.edu

Based on published and unpublished information on morphometrics, plumage appearance, behavior, and genetics, we propose that the sage-grouse first described from the Gunnison Basin, Colorado by Braun and Young (1995), be recognized as a new taxon. It fulfills the criteria for species distinction by several common species concepts including the biological species concept, the recognition concept, and the evolutionary species concept. Further, we propose that all other sage-grouse continue to be named with the English name Sage-Grouse. Our recommendation is not in agreement with the AOU Checklist Committee (2000), which recommends all other sage-grouse be named Greater Sage-Grouse. Internationally, nationally, and regionally the common name for the latter species for the past 5 years has been Northern Sage Grouse based on the relative locality from which it was first described. Following this point in the manuscript, the common name Sage-Grouse is used to refer to the species which has been previously described in the scientific literature and in professional abstracts as Northern Sage-Grouse or Sage Grouse.

**GUNNISON SAGE-GROUSE,**  
*CENTROCERCUS MINIMUS*  
NEW SPECIES

*Holotype*.—Denver Museum of Natural History (DMNH) 40722, adult (2+ years of age) male obtained by C.E.B. and J.R.Y. on 10 May 1993 approximately 23 km southeast of Gunnison, Gunnison County, Colorado. This locality is in the South Parlin area on public land administered by the Bureau of Land Management (BLM). This bird was prepared as a flat skin with skeleton. DMNH 40723 was collected on the same date and at the same location, also an adult male prepared as a flat skin with skeleton.

*Diagnosis*.—A dark brown sage-grouse with black underparts and prominent black, long, thin, specialized, ornamental contour feathers arising from the dorsal base and sides of the neck on males (lost after breeding with few apparent until molting in mid- to late November), coarsely barred brown, long tail feathers with prominent white to yellow-white bars, brown rounded wings, and feathered gray-brown tarsi. Rounded air sacs (cervical apertures) greenish-yellow within a white upper

breast, with scale-like feathers on males prominent in spring. Females smaller than males, similar in general plumage appearance but without specialized ornamental contour feathers arising from the dorsal base of the neck and without the prominent white upper breast and discernible air sacs of males. Tail length shorter than males but with same coarsely barred brown with prominent white to yellow-white bars. Both sexes smaller in mass and feather lengths than adult/yearling *C. urophasianus* with no overlap. Strut rates are slower and audible sounds differ markedly from *C. urophasianus* during breeding displays.

*Distribution*.—Gunnison Sage-Grouse currently exist in 6, possibly 7, counties in southwestern Colorado (Braun 1995, Commons 1997) and 1 county in southeastern Utah (Barber 1991). The known historic distribution (Fig. 1) of this species in Colorado was in sagebrush (*Artemisia* spp.) communities below 3000 m south of the Eagle and Colorado rivers from near Leadville (Lake County) south, and in sagebrush dominated shrub-steppe habitat into the San Luis Valley to the boundary with New Mexico and west to the Utah state line. It was known to occur in Grand and San Juan counties, Utah, south and east of the Colorado River. The distribution of the species was discontinuous within this area (Rogers 1964, Braun 1995) separated by river valleys and high forested mountains.

We hypothesize that sage-grouse formerly native to New Mexico (Bailey 1928, Merrill 1967, Hubbard 1970) belong to this species. This would exclude those trapped in Wyoming and released at a number of locations to supplement sage-grouse populations historically present in the northern areas of the state (Merrill 1967). We found no museum specimens from New Mexico (J. P. Hubbard, pers. comm.), Arizona (Phillips et al. 1983), Kansas (Goss 1883, Cable et al. 1996), or Oklahoma (Nice and Nice 1924, Sutton 1967) to test the general hypothesis that sage-grouse in all of these locations were Gunnison Sage-Grouse. The areas in northern New Mexico and extreme northeastern Arizona once had sagebrush habitats that were mostly contiguous with areas in Colorado and Utah presently occupied by Gunnison Sage-Grouse. The identity of the sage-grouse known to have oc-



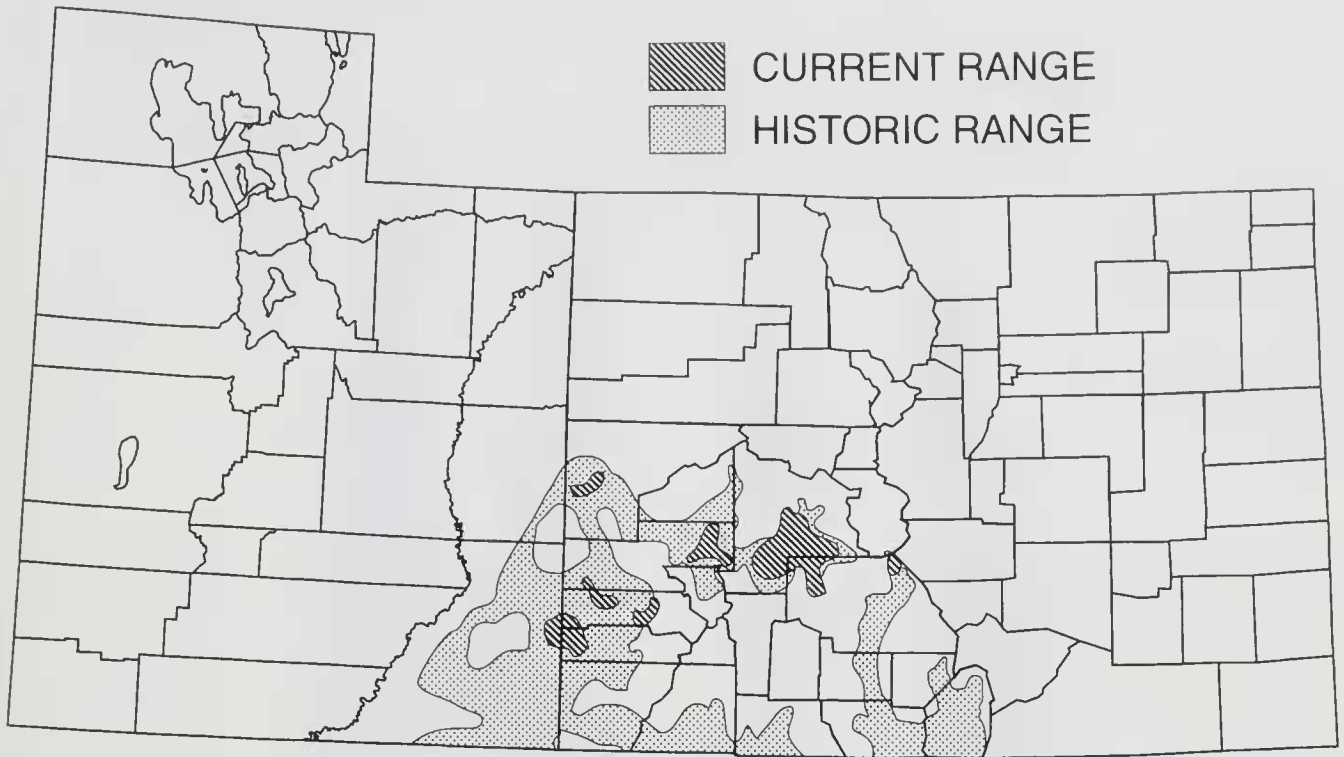


FIG. 1. Current and historic distribution of Gunnison Sage-Grouse in Colorado and Utah.

curred in extreme southwestern Kansas and adjacent northwestern Oklahoma is unknown but we postulate that they too were Gunnison Sage-Grouse because of their proximity to the current range of the species.

### MORPHOMETRICS

*Body mass.*—Mean live body mass of Gunnison Sage-Grouse captured during the breeding season (late March–late May) was 27–33% less than mean live body mass reported by Beck and Braun (1978) for Sage-Grouse in northern Colorado (Jackson County) during April–May (Table 1). Live body mass of Sage-Grouse in Jackson County, Colorado was similar to that reported for Sage-Grouse

(including *C. u. urophasianus* and *C. u. phaios*) throughout the rest of its range (Beck and Braun 1978). Differences in body mass were greatest for males (32–33%, ca 1000 g) and slightly smaller for females (27–30%, 400–500 g; Table 1).

*Length of primaries.*—Fully replaced primary feathers 10, 9, and 1 were measured in place by inserting a flexible ruler between primaries 10 and 9, 9 and 8, and 2 and 1 and recording the length from the feather insertion to the tip of the primary. Wings were available from sage-grouse harvested by hunters during September hunting seasons in the Gunnison Basin and in Jackson County, Colorado. Mean

TABLE 1. Live body mass (g) of Gunnison Sage-Grouse and Sage-Grouse from Colorado during the breeding season.

	Adult males	Yearling males	Adult females	Yearling females
Gunnison				
Mean (Sample size)	2141 (89)	1911 (21)	1204 (18)	1131 (20)
Standard error	12.6	32.7	16.3	19.4
Range	1727–2435	1622–2176	1072–1327	990–1335
Jackson County <sup>a</sup>				
Mean (Sample size)	3190 (465)	2809 (445)	1745 (221)	1551 (186)
Standard error	8.5	9.7	10.2	9.0
Range	None given			

<sup>a</sup> Data from Beck and Braun (1978).

TABLE 2. Length (mm) of primary flight feathers (P10, P9, and P1) of Gunnison Sage-Grouse and Sage-Grouse in Colorado in September.

	Adult males			Adult females		
	P10	P9	P1	P10	P9	P1
Gunnison						
Mean (Sample size)	166 (79)	216 (74)	151 (78)	139 (120)	182 (131)	130 (128)
Standard error	0.43	0.55	0.30	0.54	0.32	0.32
Range	158–179	203–226	144–159	128–155	169–196	120–138
Jackson County						
Mean (Sample size)	179 (65)	230 (54)	167 (67)	147 (100)	193 (100)	141 (100)
Standard error	0.59	0.79	0.51	0.39	0.54	0.45
Range	167–190	214–240	151–176	139–157	179–210	130–151

lengths of primaries were 8–16 mm shorter for Gunnison Sage-Grouse when compared to large bodied birds (Table 2). Differences were greater for males (6–11%) than females (5–8%). Primary lengths of Sage-Grouse in Jackson County, Colorado are similar to those of Sage-Grouse in California, Nevada, Oregon (including *C. u. urophasianus* and *C. u. phaios*), Utah, and Wyoming (C. E. Braun, unpubl. data).

**Beak size.**—Although sample sizes from all known museum specimens are small, three standard measures indicate that adult Gunnison Sage-Grouse from southwestern Colorado have shorter and narrower beaks than Sage-Grouse from northern Colorado (Table 3). Hupp and Braun (1991) found similar differences in a larger sample of culmen lengths between Gunnison Sage-Grouse and Sage-Grouse in Jackson County.

**Tail length.**—Length of tail feathers of males [ $\bar{x} = 347 \pm 0.5$  (SE),  $n = 36$ ] is longer in Gunnison Sage-Grouse than in other Sage-Grouse (generally <315 mm), although this character is easily altered by wear. Both sexes of Gunnison Sage-Grouse have clearly defined

white or cream bars (width = 5–7 mm) on the rectrices, unlike the indistinct barring on the tail feathers of other Sage-Grouse (Fig. 2). Thus, the elaborate neck feathers of males and the uniquely barred rectrices are the best field identification characters for the Gunnison Sage-Grouse.

## PLUMAGE

Outside the breeding season, sage-grouse throughout western North America are similar in appearance. Overall coloration varies from gray-brown to darker brown within a population and changes seasonally because of feather fading resulting from exposure to the environment and molt replacement of body feathers (C. E. Braun, pers. obs.). Sage-grouse in southwestern Colorado and southeast Utah differ from all other studied populations in length and thickness of modified feathers on the dorsal surface of the back and sides of the neck of males during the breeding season (Fig. 3). The elaborate long, thin black specialized ornamental contour body feathers that arise from the dorsal base of the neck of Gunnison Sage-Grouse adult males (range 120–173 mm,  $\bar{x} = 146 \pm 0.2$ ,  $n = 38$ ) and 3–6 mm wide give an appearance of a black “ponytail” when displayed. In contrast, Sage-Grouse have shorter and thinner (generally <115 mm long and 1 mm wide) dorsal neck feathers.

## BEHAVIOR

Gunnison Sage-Grouse are similar to Sage-Grouse in that they have a lek mating system. Breeding behavior is initiated in early spring (generally in March) and terminates in late May. Many of the attributes that distinguish

TABLE 3. Mean beak measures (mm) of museum<sup>a</sup> specimens from Gunnison Sage-Grouse and Sage-Grouse in Colorado. Sample size in parentheses.

	Adult male		Adult female	
	Gunnison	Northern Colorado	Gunnison	Northern Colorado
Culmen	31.7 (3)	39.1 (4)	28.0 (4)	30.6 (9)
Nostril to tip	14.3 (3)	16.6 (4)	12.9 (4)	14.5 (9)
Width	16.0 (3)	21.7 (4)	13.8 (4)	17.1 (9)

<sup>a</sup> Sample sizes of museum specimens of adult Sage-Grouse from Colorado are small.



FIG. 2. Rectrices of Gunnison Sage-Grouse (b and d) and Sage-Grouse (a and c). Drawn from life by D. L. Rieden.

male Gunnison Sage-Grouse from Sage-Grouse males are sexually dimorphic traits used during mating displays on the lek (Young et al. 1994). Gunnison Sage-Grouse perform their courtship displays at slower rates (Young et al. 1994). They possess a different mating call in which they pop their air sacs nine times instead of twice as does the Sage-Grouse (Young et al. 1994). Previous studies of sage-grouse indicate that some acoustical aspects of the mating display influence male mating success (Gibson and Bradbury 1985, Gibson et al. 1991). On average, only 10–15% of the adult males breed on the lek each season (J. R. Young, pers. obs.). Yearling and adult females breed; yearling males probably breed rarely.

Male courtship calls of Gunnison Sage-Grouse have been described by Young and co-workers (1994), and recordings of males and females have been deposited with the Library

of Natural Sounds (LNS) at the Cornell Laboratory of Ornithology. In general, male Gunnison Sage-Grouse have mating vocalizations that are similar in duration, but different in structure from male mating vocalizations of Sage-Grouse. Gunnison Sage-Grouse females produce a variety of vocalizations on the lek; however, they have not been compared with vocalizations from female Sage-Grouse. Both male and female Gunnison Sage-Grouse vocalize off the lek and in contexts similar to those noted in the other species (J. R. Young, pers. obs.). No vocalization recordings have been obtained for either sex off the lek.

Young (1994) found that females in the Gunnison Basin and northern Colorado avoided playbacks of male courtship vocalizations that differed from the vocalizations of their local population. She concluded that differences in male courtship vocalizations were likely a barrier to mating between Gunnison





FIG. 3. Lateral views of head and neck of Gunnison Sage-Grouse (lower) and Sage-Grouse (upper). Drawn from life and photos by D. L. Rieden.

Sage-Grouse and Sage-Grouse. Thus, Gunnison Sage-Grouse appear to be reproductively isolated based on male courtship vocalizations, which act as pre-mating isolating mechanisms. Divergence of mating behaviors coupled with geographical isolation may result in the rapid evolution of a new species through sexual selection (Lande 1981, Kaneshiro and Boake 1987).

### GENETICS

Sequence information from 141 bp of region I of the rapidly evolving mitochondrial control region was gathered from 201 individuals of 5 Sage-Grouse and 4 Gunnison Sage-Grouse populations within Colorado (Kahn et al. 1999, Oyler-McCance et al. 1999). Sage-grouse in general were found to have four dominant haplotypes in all populations, only one of which was found in the Gunnison Sage-Grouse populations. The Gunnison Sage-Grouse populations had one haplotype that was unique. A similar distinction between Gunnison Sage-Grouse and Sage-Grouse was found using 4 nuclear microsatellites (Oyler-McCance et al. 1999).

Both mitochondrial and nuclear markers revealed there were no significant differences among the Sage-Grouse populations indicating gene flow among them. Within the Gunnison Sage-Grouse populations, however, most pairwise comparisons with other populations showed significant differences among populations suggesting there is some population differentiation, probably as a result of their small population sizes and isolation (Oyler-McCance et al. 1999).

Thus, DNA sequence information from the mitochondrial and nuclear genomes supports the hypothesis that there is a barrier to gene flow between Gunnison Sage-Grouse and Sage-Grouse populations. This implication is made on the basis of two observations. First, there are frequency differences of shared mitochondrial haplotypes and shared microsatellite alleles between Sage-Grouse and Gunnison Sage-Grouse. Second, there are 3 microsatellite alleles and 1 mitochondrial haplotype that have remained unique to the small-bodied populations, based on the current sampling numbers.

We suggest these genetic differences are the result of reproductive isolation that is rein-

forced by (at minimum) the behavioral isolating mechanisms discussed previously. Hence, we conclude these are separate species according to the biological species concept. However, there are no fixed sequence differences between the two taxa so that based on the molecular data alone, an interpretation that these are species according to the phylogenetic species concept is obviated. The molecular differences we observed between these taxa are among the smallest observed for most vertebrates (Avice and Walker, 1999). Avice and Walker (1999) suggested that genealogical (phylogenetic) and reproductive traits are intimately intertwined, as are the related biological and phylogenetic species concepts. It appears the Gunnison Sage-Grouse provides an example of an intermediate stage of speciation where reproductive isolation is in place, but other molecular differences continue to diverge. Such a situation can be expected when morphological or behavioral change occur rapidly relative to changes in alternate haplotypes/alleles that are not related to reproductive isolation. Based on the extreme sexual dimorphism and the small number of males that obtain most of the matings (Wiley 1973, Vehrencamp et al. 1989), sexual selection is likely the predominant selective force.

### HABITAT AND CONSERVATION STATUS

*Habitat.*—Nesting, brood-rearing, and summer habitats used by Gunnison Sage-Grouse have been described by Young (1994) and Commons (1997). Nesting success is highest in areas where forb and grass covers are found below a sagebrush (15–30%) canopy (Young 1994). Average clutch size ( $n = 24$ ) is  $6.8 (\pm 0.7)$  eggs and eggs average  $54.5 (\pm 1.4)$  mm long  $\times$   $38.0 (\pm 0.7)$  mm diameter. Clutch and egg sizes are within the range reported for Sage-Grouse (Schroeder et al. 1999). In winter Gunnison Sage-Grouse are restricted to areas with substantial cover (15–30%) of big sagebrush (*A. tridentata vaseyana*, *A. t. wyomingensis*), black sagebrush (*A. nova*), and low sagebrush (*A. arbuscula*) intermixed with native grasses and forbs and associated riparian habitats (Hupp and Braun 1989). Their winter habitat differs from Sage-Grouse; they use areas with more deciduous shrubs such as Gambel oak (*Quercus gambelii*) and serviceberry (*Amelanchier*) as well as areas invaded by pi-

ñon (*Pinus*) and juniper (*Juniperus*) at elevations of 1800–2800 m. Sagebrush leaves are probably the principle food from November into April, whereas forbs and insects are commonly eaten in summer. In disturbed and fragmented habitats, Gunnison Sage-Grouse forage and roost in cultivated fields of alfalfa, wheat, and beans (Young 1994, Commons 1997). Detailed analyses of their diet across seasons have not been done.

*Conservation status.*—The historic abundance is unknown but we estimate that it was several orders of magnitude larger than at present based on historical documents and interviews. Eight populations are known, totaling fewer than 5000 breeding birds of which fewer than 3000 occur in the Gunnison Basin, Colorado. Some populations are small, fewer than 150 breeding birds and several former populations are known to have become extirpated since 1980 (Braun 1995). Fewer than 150 Gunnison Sage-Grouse are known to occur in Utah. Gunnison Sage-Grouse are at risk of extinction because of habitat loss, fragmentation, and degradation (Braun 1998, Oyler-McCance 1999). In the Gunnison Basin, the average number of males attending leks has declined by more than 60% since 1953 (J. R. Young, unpubl. data). All eight small populations have high potential for inbreeding and populations that have been examined have low genetic diversity in the nuclear and mtDNA genomes (Young 1994, Kahn et al. 1999, Oyler-McCance et al. 1999). A petition has been submitted requesting listing under the federal Endangered Species Act of 1973. The Colorado Division of Wildlife, Bureau of Land Management, and other agencies within the U.S. Department of Interior, working with local agencies, interest groups, and private citizens, have developed locally derived and supported conservation plans. Some aspects of those plans are being implemented for six populations in Colorado. A conservation plan is under development for Gunnison Sage-Grouse in San Juan County, Utah, and plans are being finalized for two of the three populations in Colorado that lack approved plans. Submission of this manuscript was deliberately delayed for several years to allow completion and implementation of conservation plans to help protect the new species. With completion and implementation of useful conserva-

tion plans, it is our hope that Gunnison Sage-Grouse will continue to exist for the foreseeable future.

### ETYMOLOGY

This new species is named *Centrocercus minimus* because of its relatively small size. The English name, Gunnison Sage-Grouse, is derived from the general area (Gunnison Basin, Gunnison County, Colorado) where the species was first recognized as being different and intensively studied, and in recognition of the effort by the local citizens who seek to promote its conservation.

### ACKNOWLEDGMENTS

Numerous individuals have been helpful with our studies of Gunnison Sage-Grouse and we thank all who helped with this long-term effort. We thank all that came out with us at strange hours of the night to trap and record data during early dawns (especially C. L. Henkel, L. A. Higgins, J. A. Hill, D. L. Rieden, and T. J. Swedlund) and those whose research has contributed to our knowledge of Gunnison Sage-Grouse including M. L. Commons and S. H. Ly. We appreciate the willingness of private landowners to work with us in planning and implementing conservation actions designed to stop and reverse the decline in distribution and abundance of this unique species. Personnel of the BLM, especially M. W. Stiles (Montrose) and J. D. Almand (Washington, D.C.) were helpful with policy issues which facilitated our work at local levels in southwestern Colorado. Other employees of the BLM that were particularly helpful were J. A. Capodice, H. D. Countess, J. A. Hayes, S. J. Hayes, and S. L. Thode. All trapping, banding, and collections were under permits issued by the Colorado Division of Wildlife. The Colorado Division of Wildlife was helpful with logistics and support and we especially thank Area Managers J. D. Houston and J. A. Young, and District Wildlife Managers M. C. Coghill, P. J. Creeden, D. B. Harper, T. K. Henry, D. B. Homan, P. B. Jones, and T. J. Spezze. We thank D. L. Rieden and D. Radovich for their artistic talents and J. W. Bradbury, R. D. Howard, and S. L. Vehrencamp for advice and support. We also thank W. G. Alther and C. R. Preston of the Denver Museum of Natural History for advice and preparation of the specimens. The Colorado Division of Wildlife supported this work under Federal Aid in Wildlife Restoration Projects W-152-R and W-167-R. Research support was also obtained from the Rob and Bessie Welder Wildlife Foundation, Indiana Academy of Science, Sigma Xi, American Museum of Natural History Chapman Fund, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Purdue University, and Western State College. This manuscript was improved by the reviews of R. C. Banks, J. P. Hubbard, and an anonymous reviewer.



## LITERATURE CITED

- ALDRICH, J. W. 1946. New subspecies of birds from western North America. *Proc. Biol. Soc. Wash.* 59:129–136.
- ALDRICH, J. W. 1963. Geographic orientation of American Tetraonidae. *J. Wildl. Manage.* 27:529–545.
- ALDRICH, J. W. AND A. J. DUVALL. 1955. Distribution of American gallinaceous game birds. U.S. Dept. Inter. Fish Wildl. Serv. Circ. 34:1–30.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, Fifth ed. Lord Baltimore Press, Inc., Baltimore, Maryland.
- AOU CHECKLIST COMMITTEE. 2000. Forty-second supplement to the American Ornithologists' Union Checklist of North American birds. *Auk* 117:847–858.
- AVISE, J. C. AND D. WALKER. 1999. Species realities and numbers in sexual vertebrates: perspectives from an asexually transmitted genome. *Proc. Natl. Acad. Sci. USA* 96:992–995.
- BAILEY, F. M. 1928. Birds of New Mexico. New Mexico Dept. Game and Fish, Santa Fe; Judd & Deweiler Press, Inc., Washington, D.C.
- BARBER, H. A. 1991. Strutting behavior, distribution and habitat selection of Sage Grouse in Utah. M.S. thesis, Brigham Young Univ., Provo, Utah.
- BECK, T. D. I. AND C. E. BRAUN. 1978. Weights of Colorado Sage Grouse. *Condor* 80:241–243.
- BRAUN, C. E. 1995. Distribution and status of Sage Grouse in Colorado. *Prairie Nat.* 27:1–9.
- BRAUN, C. E. 1998. Sage Grouse declines in western North America: what are the problems. *Proc. West. Assoc. State Fish Wildl. Agencies* 78:139–156.
- BRAUN, C. E. AND J. R. YOUNG. 1995. A new species of Sage Grouse in Colorado. *Abstr. Wilson Ornithol. Soc. and Virginia Soc. Ornithol.*, Williamsburg, Virginia.
- CABLE, T. T., S. SELTMAN, AND K. J. COOK. 1996. Birds of Cimarron National Grassland. U.S. Dept. Agric., Forest Serv. Gen. Tech. Rep. RM-GTR-281:1–108.
- COMMONS, M. L. 1997. Movement and habitat use by Gunnison Sage Grouse (*Centrocercus minimus*) in southwestern Colorado. M.S. thesis, Univ. of Manitoba, Winnipeg.
- GIBSON, R. M. AND J. W. BRADBURY. 1985. Sexual selection in lekking Sage Grouse: phenotypic correlates of male mating success. *Behav. Ecol. Sociobiol.* 18:117–123.
- GIBSON, R. M., J. W. BRADBURY, AND S. L. VEHCAMP. 1991. Mate choice in lekking Sage Grouse revisited: the roles of vocal display, female site fidelity and copying. *Behav. Ecol.* 2:165–180.
- GOSS, N. S. 1883. A catalogue of the birds of Kansas. Kansas Publication House, Topeka.
- HUBBARD, J. P. 1970. Check-list of the birds of New Mexico. *New Mexico Ornithol. Soc. Publ.* 3:1–103.
- HUPP, J. W. 1987. Sage Grouse resource exploitation and endogenous reserves in Colorado. Ph.D. diss., Colorado State Univ., Fort Collins.
- HUPP, J. W. AND C. E. BRAUN. 1989. Topographic distribution of Sage Grouse foraging in winter. *J. Wildl. Manage.* 53:823–829.
- HUPP, J. W. AND C. E. BRAUN. 1991. Geographic variation among Sage Grouse in Colorado. *Wilson Bull.* 103:255–261.
- JOHNSGARD, P. A. 1973. Grouse and quails of North America. Univ. of Nebraska Press, Lincoln.
- KAHN, N. W., C. E. BRAUN, J. R. YOUNG, S. WOOD, D. R. MATA, AND T. W. QUINN. 1999. Molecular analysis of genetic variation among large- and small-bodied Sage Grouse using mitochondrial control-region sequences. *Auk* 116:819–824.
- KANESHIRO, K. Y. AND C. R. B. BOAKE. 1987. Sexual selection and speciation: issues raised by Hawaiian *Drosophila*. *Trends Ecol. Evol.* 2:207–211.
- LANDE, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* 78:3721–3725.
- MERRILL, G. W. 1967. Sage Grouse. Pp. 111–113 in *New Mexico wildlife management*. New Mexico Dept. Game and Fish, Santa Fe.
- NICE, M. M. AND L. B. NICE. 1924. The birds of Oklahoma. Univ. of Oklahoma Bull., Norman.
- OYLER-McCANCE, S. J. 1999. Genetic and habitat factors underlying conservation strategies for Gunnison Sage Grouse. Ph.D. diss., Colorado State University, Fort Collins.
- OYLER-McCANCE, S. J., N. W. KAHN, K. P. BURNHAM, C. E. BRAUN, AND T. W. QUINN. 1999. A population genetic comparison of large- and small-bodied sage grouse in Colorado using microsatellite and mitochondrial DNA markers. *Mol. Ecol.* 8:1457–1466.
- PHILLIPS, A., J. MARSHALL, AND G. MONSON. 1983. The birds of Arizona. Univ. of Arizona Press, Tucson.
- ROGERS, G. E. 1964. Sage Grouse investigations in Colorado. Co. Game Fish Parks Dept. Tech. Publ. 16:1–132.
- SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage Grouse (*Centrocercus urophasianus*). In *The birds of North America*, no. 425 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologist's Union.
- SUTTON, G. M. 1967. Oklahoma birds: their ecology and distribution with comments on the avifauna of the southern Great Plains. Univ. of Oklahoma Press, Norman.
- VEHCAMP, S. L., J. W. BRADBURY, AND R. M. GIBSON. 1989. The energetic cost of display in male Sage Grouse. *Anim. Behav.* 38:885–896.
- WILEY, R. H. 1973. Territoriality and non-random mating in Sage Grouse, *Centrocercus urophasianus*. *Anim. Behav. Monogr.* 6:85–169.
- YOUNG, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence of Sage Grouse. Ph.D. diss., Purdue Univ., West Lafayette, Indiana.
- YOUNG, J. R., J. W. HUPP, J. W. BRADBURY, AND C. E. BRAUN. 1994. Phenotypic divergence of secondary sexual traits among Sage Grouse populations. *Anim. Behav.* 47:1353–1362.